BREVIORA

Museum of Comparative Zoology

Cambridge, Mass. 30 April, 1969 Number 319

COMPETITIVE EXCLUSION AMONG ANOLES (SAURIA: IGUANIDAE ON SMALL ISLANDS IN THE WEST INDIES[1]

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Abstract. Each of the Greater Antilles has been a largely independent center of anole radiation and there has been little exchange of species between them. Together they are the source areas from which the other islands of the Antilles have been colonized. The area and number of anole species known from 122 of these smaller islands on 44 banks are tabulated.

There are two kinds of small islands in the West Indies. The islands of one class show a correlation between area and number of anole species, and the larger islands may have up to 4 or 5 species. Islands of the other class do not show an area effect and never have more than 1 or 2 species.

The first class includes the islands of the Great Bahama Bank and the islands fringing the Greater Antilles and lying on the same bank as one or another of them. The second class includes the Lesser Antilles and the small isolated islands of the Caribbean.

The difference between the two classes seems to be a result of their Pleistocene history and the way in which they received their anole faunas. The islands of the first class were all connected or very close to a source area during the Pleistocene sea level minima and so probably received their anoles overland and more or less at the same time. The area effect now seen was probably produced by differential extinction subsequent to a sea level rise and separation of the various islands. The islands of the second class must all have been colonized over an appreciable water gap.

The absence of islands with more than 1 or 2 species in this second class cannot be due to ecology, size, distance, or species of anoles involved, since some of the islands are large, diverse, and no further from a suitable source than some fringing islands are today. The data suggest that a first species finds it relatively easy to colonize an island. A second species finds it difficult, and a third may find it impossible, even though three species may coexist on a very small and ecologically impoverished island if they have colonized it overland. The exclusion effect occurs not because of the difficulties in reaching the island, but because of the difficulties in establishment. The latter are the result of inter-specific competition in which an

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[1] Research supported in part by NSF Grant GB-6944.

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already established species can exclude an invader even though if both were established together they might coexist. It is suggested that competitive exclusion may also explain the small number of exchanges of species among the Greater Antilles.

This paper deals with the factors influencing the number of species of *Anolis* per small island in the West Indies. Darlington (1957) relates faunal size and complexity in the West Indies to island area and to distance from the postulated source area of Central America. However true these generalizations are for the fauna as a whole, they must be modified for the genus *Anolis*: first, because the West Indies have been a center of speciation and have not received their modern fauna directly from Central America and, second, because there is a class of small West Indian islands that have only one or two species of *Anolis* regardless of area or distance from source islands. The following discussion of the distribution of a single genus in one area is an approach to the theoretical problems of the zoogeography of archipelagos that I hope is complementary to the more mathematical treatments of Hamilton, Barth, and Rubinoff (1964), MacArthur and Wilson (1967), and others.

There are approximately 3,000 islands in the West Indies. Many of the islands stand on more or less extensive banks and are separated from one another or from one of the Greater Antilles by only shallow water. When the sea level was lowered during the last Pleistocene glaciation, the banks must have largely been exposed. At that time the islands on each bank must have been connected to one another by dry land, so that an exchange of land faunas was possible. The anole faunas of the islands on each bank are very similar to one another. The water between the banks is very deep, and there is no possibility that islands on different banks were connected during the Pleistocene.

During the interglacial period that preceded the last glaciation, the sea level was higher than it is at present, and the maximum probably was high enough to submerge completely many of the low-lying West Indian islands and exterminate any anoles living there.

Anolis is represented in the West Indies by about 100 species, more species than are known for any other genus of land vertebrates in the area. These species may be the results of as few as two overwater invasions, one from Central America into Jamaica or Cuba and the other from South America into Puerto Rico or perhaps Hispaniola. Here and below the conclusions of Etheridge (1960) and Williams (personal communication) on the relationships within the genus *Anolis* have been followed.

Each of the four Greater Antilles has been a largely independent center of evolution for anoles. Cuba has 23 species of *Anolis,* Hispaniola 21 species, Jamaica 7 species, and Puerto Rico 10 species. Despite the fact that several of these species have crossed large water gaps to live on distant small islands, only one species is shared by two of the large islands. Even in the more distant past, the number of colonizations between the Greater Antilles was small. Only eight such events are necessary to explain the relationships between living forms: four between Puerto Rico and Hispaniola; two between Hispaniola and Cuba; two between Cuba and Jamaica. On the four large islands, speciation has been largely within and not between islands.

The Greater Antilles, with their older and richer anole faunas, are probably the source areas from which the smaller (some only recently habitable) West Indian islands have been colonized. An anole invading one of the Greater Antilles from a small island is probably even rarer than the invasion of one of the Greater Antilles by an anole from another.

Anoles have repeatedly crossed water gaps. They have not only reached and spread throughout the West Indies, but one West Indian species has reached the coast of Central America and another the Bay Islands of Honduras. It has been suggested that anoles may be blown from island to island in hurricanes or float across in rafts of vegetation carried by ocean currents. Perhaps they travel in the masses of debris and vegetation that are torn loose from a hurricane-lashed shore and blown out to sea. The heavy rains that accompany hurricanes would reduce the danger from salt water during the journey.

On the assumption that the large islands have been the source areas, most but not all colonizations have been from east to west, which is the general direction of both ocean currents and prevailing winds, as well as the storm track of many hurricanes (see Fig. 1).

Data on area and number of *Anolis* present have been collected for 126 small islands on 44 banks. Anole distributions from Barbour (1937), Cochran (1934, 1941), Grant (1932a, 1932b, 1936, 1937), Grant and Roosevelt (1932), Oliver (1948), Ruibal (1964), Underwood and Williams (1959) have been supplemented by the collections in the Museum of Comparative Zoology and unpublished information from the files of their curator, Dr. Ernest E. Williams. Mr. J. D. Lazell, Jr., and Dr. Albert Schwartz generously shared the results of their extensive field experience. Thanks are due to all three. Information on island areas was taken from the Columbia Lippincott Gazetteer of the World and

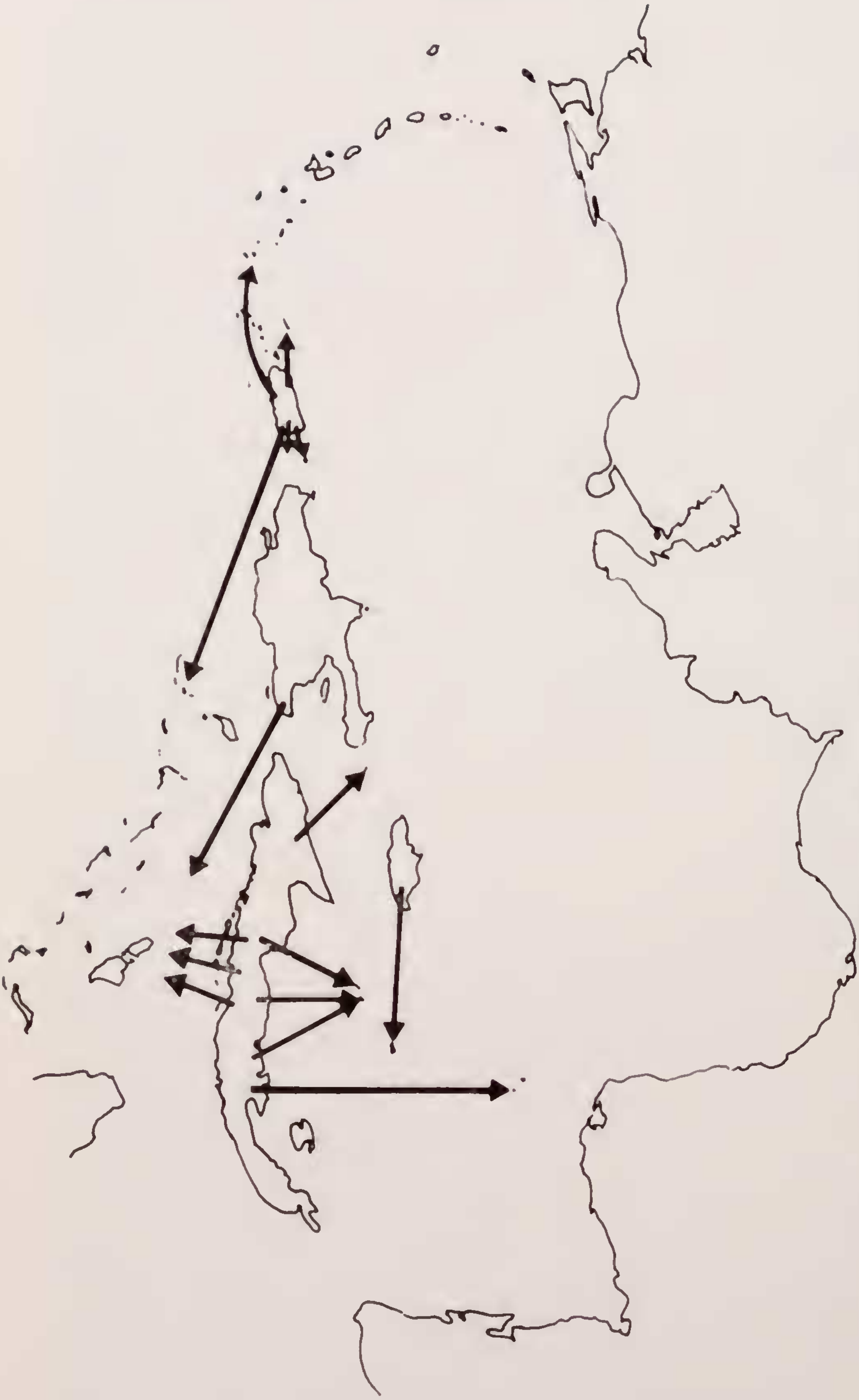

Fig. 1. The major overseas colonizations by *Anolis* of the West Indian isolated islands, the Bahamas, and the Lesser Antilles from the Greater Antilles. The most probable directions are indicated by arrows.

U. S. Hydrographic Office charts. The data are given in Table 1. Almost all the major islands are included; the number of smaller ones could be increased greatly, but there is no suggestion that this would change the picture.

The smaller islands of the West Indies fall into four geographical categories: (1) the islands fringing the Greater Antilles; (2) the Lesser Antilles; (3) the isolated islands of the Antilles; and (4) the islands of the Bahamas. Each of these groups shows a somewhat different pattern of anole distribution.

(1) The fringing islands of the Greater Antilles stand on a bank with one or another of the four Greater Antilles and are separated from it by only shallow water. Most are close to the associated large island, but some of the Virgin Islands are almost 100 miles from Puerto Rico. These islands vary ecologically from very simple to moderately complex. I have data on 44 islands in this group, all inhabited by anoles.

The fringing islands show a definite area effect, i.e., size of island and number of species are directly correlated (Fig. 2). Many are low, and most must have been submerged during the last Pleistocene sea level maximum. During the last Pleistocene sea level minimum, these islands must have become hills on the coastal plains of the Greater Antilles and been inhabited by the common lowland species of *Anolis*. After the sea level rose, the larger islands (more than 25 square miles) kept their original three to five species, but on the smaller islands there appears to have been a tendency for species to become extinct. The number that remains is related in part to island area, and the very smallest islands (less than 1 square mile) frequently now have only a single species left. On none of these islands has there been any appreciable differentiation except for the endemic, *A. roosevelti,* on Culebra.

(2) The Lesser Antilles extend in a 500 mile arc from just east of the Virgin Islands south almost to Trinidad and Tobago. Many reach altitudes of several thousand feet and show a variety of climatically different habitats with rich floras. I have data on 33 islands on 16 different banks, all inhabited by anoles.

Comparing these islands among themselves there is no apparent area effect. Five of the banks have islands with two species, the islands on the remaining 11 banks have only a single species (excluding certain introductions by man). The Lesser Antilles have been colonized by two different stocks. One, the *bimaculatus* species group, including *wattsi,* has spread throughout the Northern Lesser Antilles, crossing at least nine water gaps. It probably came from the Greater Antilles, though the ancestral species has either disappeared or changed so much that it is unrecognizable. The stock has differentiated on every island, and taxonomists differ on how many populations have reached the species level. On several islands these anoles show marked geographical variation within the island (Lazell, 1962, 1964). Though the *bimaculatus* group has been in the Lesser Antilles a long time, there seem to have been very few cases of double invasions. On only the three northernmost banks do two species (one of them *wattsi*) occur together.

The second stock, the *roquet* group, has invaded the Lesser Antilles from the south, crossing at least seven water gaps, but it is not known to be closely related to any living South American species. There are two banks on which two species of this group coexist. The degree of differentiation between islands is less in this group than in the *bimaculatus* group.

(3) The isolated islands are those islands or small groups of islands scattered throughout the West Indies and separated from all other islands by very deep water. Most are low and quite simple ecologically. Some are very far from any source area, others are quite close. I have data on 11 islands, on 9 banks, all inhabited by anoles. (There are also a very few, very small, isolated cays [e.g. Pedro Cays, Aves Island] that are uninhabited; they are the only islands in the West Indies known to lack anoles.)

These islands show no area effect. One island has two species of anoles, the others a single species. Most of these islands were probably submerged during the Pleistocene sea level maximum and colonized overwater since their emergence. All of these islands are occupied by species that are conspecific with or clearly derived from a species now living on one of the Greater Antilles. The one exception is *acutus* on St. Croix, probably derived from a Puerto Rican stock but not from one of the living species.

(4) The Bahamas are a large group of islands stretching for some six hundred miles in an elongate cluster from Florida, along the northeast coast of Cuba, almost to Hispaniola. They are all low islands with little ecological diversity and were probably all submerged during the last Pleistocene sea level maximum. The islands lie on a number of banks of various sizes. I have data on 53 islands on 15 banks, all inhabited by anoles.

The largest bank is the Great Bahama Bank. During the Pleistocene sea level minimum, its many islands must all have been part of a single very large island lying next to Cuba. The present islands show an area effect very like that of the fringing islands. The larger islands on this bank are inhabited by four species of anoles, three from Cuba (*sagrei, carolinensis,* and *angusticeps*) and one from Hispaniola (*distichus*). These species must have reached the bank overwater and then probably spread through it overland.

The remaining Bahamas lie on a number of smaller banks. Of the 14 banks for which I have data, the islands on 10 are occupied by a single species and on 4 by two species. Many of these islands are much larger and at least as varied ecologically as some of those on the Great Bahama Bank that are occupied by four species of anoles.

The Bahamas on other banks that lie close to the Great Bahama Bank are occupied by one or two of the anoles that occur on the Great Bahama Bank. The Bahamas farther southeast are occupied by a single endemic species, *scriptus*. The ancestors of *scriptus* may have reached the Bahamas in a single long overseas crossing from Puerto Rico, where its very close relative, *cristatellus,* occurs, though it may have come from a now extinct form on Hispaniola. *A. scriptus* does not occur with any other anole, though it lives on West Plana Cay only ten miles from East Plana Cay, which is occupied by *A. carolinensis.*

From this survey it appears that, on the basis of the size of their anole faunas, there are two kinds of small islands in the West Indies. The first class of island includes the fringing islands of the Greater Antilles and the islands of the Great Bahama Bank. These clearly show an area effect and only the smallest have a single-species fauna (Fig. 2, *upper*). The second class of island includes all of the Bahamas off the Great Bahama Bank, the Lesser Antilles, and the isolated islands (Fig. 2, *lower*). These show little if any area effect, and even the largest islands have only one or two species.

The difference in numbers of anoles between these two types of islands cannot be explained on the basis of differences in their ecological diversity or carrying capacity. The Lesser Antilles, with only one anole species, are larger, much richer, and more varied ecologically than are many fringing islands with three or four species of anoles. Within the Bahamas there seems to be no difference in the ecology between the islands on the Great Bahama Bank, where four species coexist, and those on other banks, where only one or two species occur together. The difference cannot be in behavioral or ecological peculiarities of the species involved, for the species that replace one another in some of the Bahamas occur

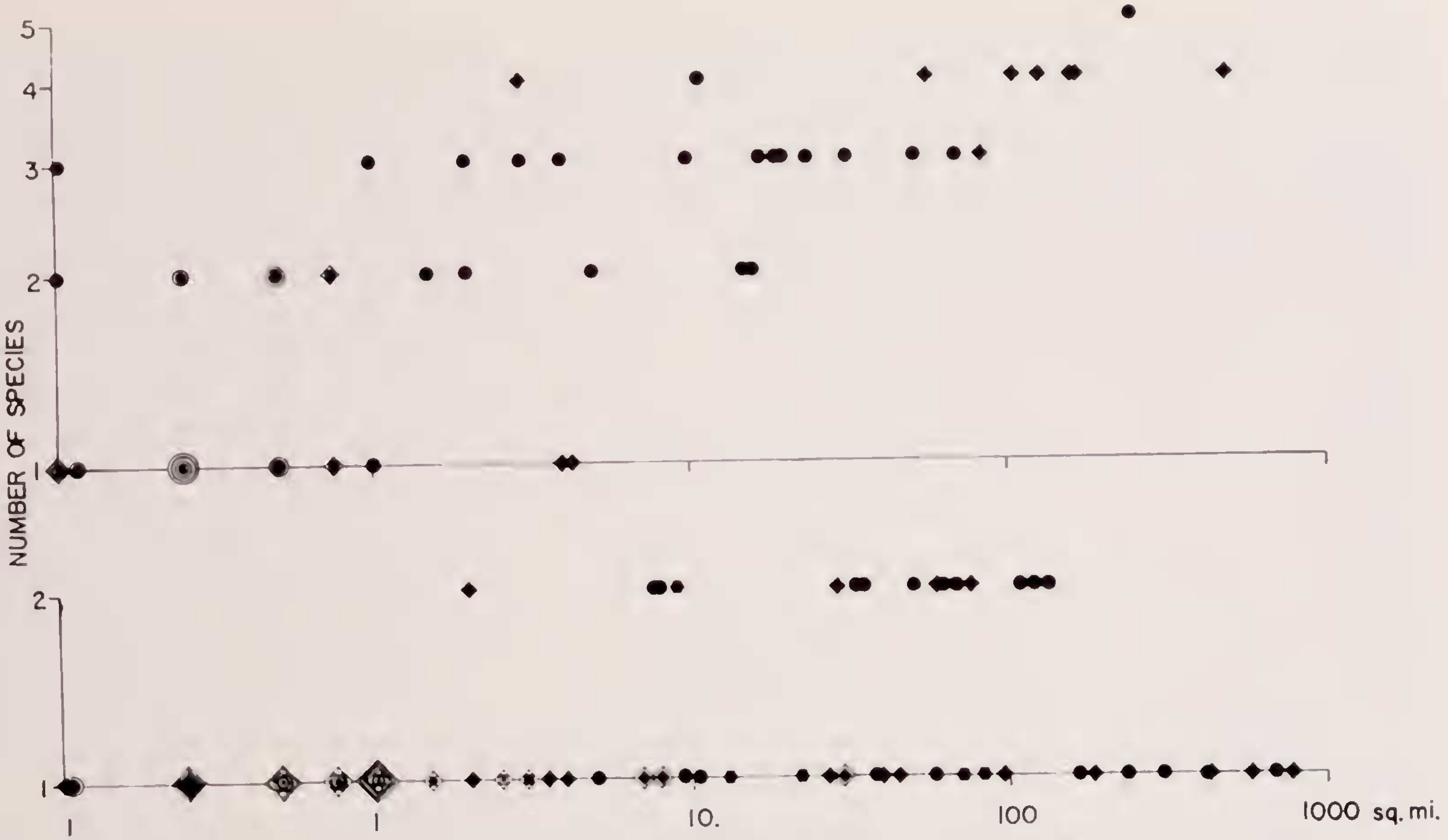

Fig. 2. Island area and number of species of *Anolis* on the small West Indian islands. Each symbol represents an island. *Upper.* The islands of the Great Bahama Bank (diamonds) and those fringing the four Greater Antilles (circles). These show a clear area effect. *Lower.* The Lesser Antilles (circles), the West Indian isolated islands (hexagons), and the Bahamas off the Great Bahama Bank (diamonds). These show little area effect.

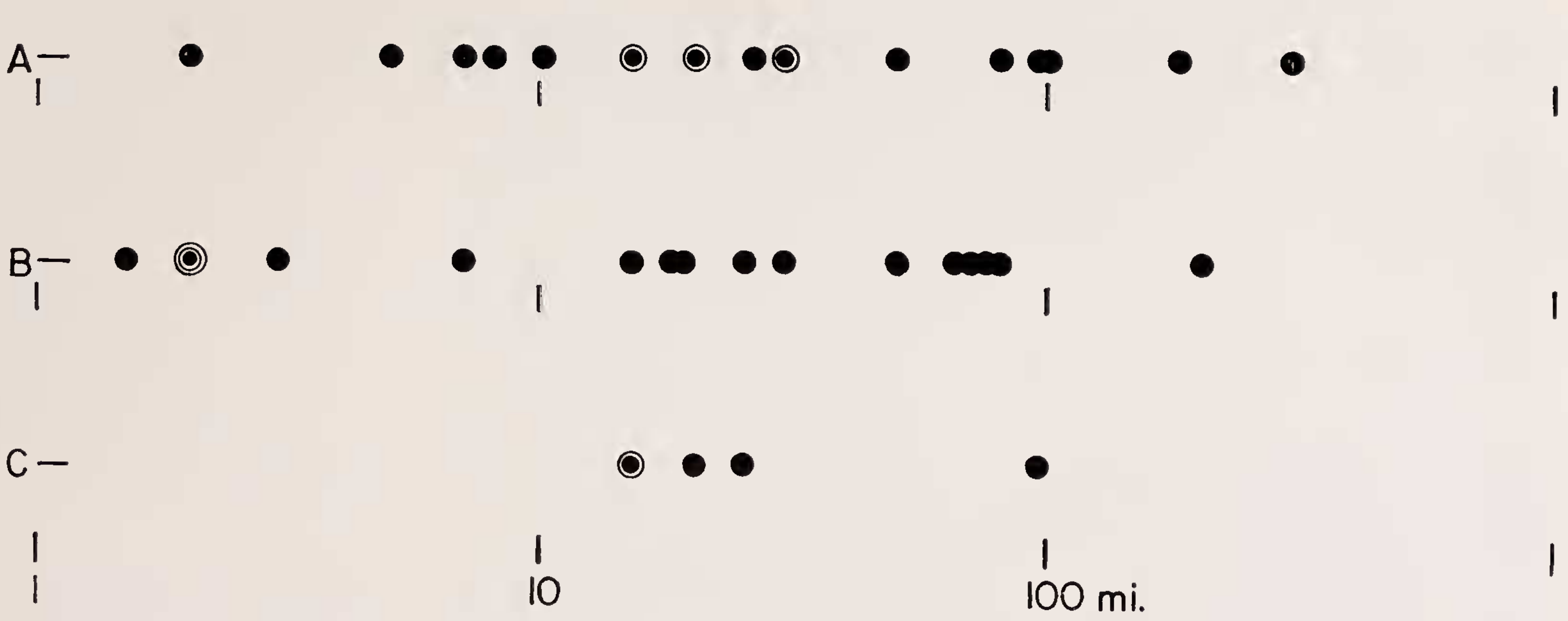

Fig. 3. Distance from source and number of species of *Anolis* on the West Indian isolated islands and the Bahamas off the Great Bahama Bank. Each symbol represents a bank of islands. Distances are measured between one hundred fathom lines and are approximate. *A*. One-species islands — the distance from the nearest point from which their species could have come. *B*. One-species islands — the distance from the nearest point from which an additional species could come. *C*. Two-species islands — the distance from the nearest point (or points) from which their species could have come. The similarity of these three sets of distances demonstrates that it is not distance from the source areas that distinguishes the one-species from the two-species islands.

together on the Great Bahama Bank. The width of present-day water gaps is another factor that will not explain the differences in number of species (Fig. 3).

The factors that do seem important in causing the difference are related to the Pleistocene history of the islands and the manner in which they were colonized, either over land or over water. The fringing islands could, and probably did, receive their several species of anoles over land, all more or less at the same time, during the period of lower sea level. Each species was represented by many individuals. The present islands of the Great Bahama Bank probably received their faunas in the same way, though the bank itself must have been colonized over water. The isolated islands, the Lesser Antilles, and the Bahamas off the Great Bahama Bank probably received their anoles over water. The species probably arrived separately and only one or a very few individuals reached an island at one time.

One species or another of *Anolis* has succeeded in colonizing every West Indian island of more than a square mile in area, and almost all of the even smaller ones have been colonized, as well. It can be suggested that the reason so few of these islands have two species and none three is that the additional species have never reached them. But if the difficulty of reaching the islands were the explanation, then one would find that the islands that were easier to reach, because they were down wind, down current, or close to the source, would have more species than the islands that were harder to reach. This is not the case. The position of an island relative to the source area has more effect on *what* species will reach it than on how many. Figure 3 shows there is no simple correlation between number of species and distance from source area.

The limited anole faunas must result from interactions between species. Apparently a species established on an island makes it more difficult for the second species that reaches the island to establish itself. If the second species is successful, it is even more difficult for additional species to establish. I would suggest that, because of the low probability of overwater colonization of an island, the first species reaching it has time to occupy it completely before any other species lands. The only island large enough and close enough to the source areas for several species to colonize it before any one of them occupied it completely was the Pleistocene island that is now the Great Bahama Bank. Once the four species were established, they were able to coexist, so that the modern islands show an area effect like fringing islands rather than like the other Bahamas. The phenomenon of an established species of *Anolis* preventing a newly arrived species from colonizing can be called competitive exclusion, because it must be the result of interspecific competition.

The four species that exclude one another on the Bahamas off the Great Bahama Bank were studied by Oliver (1948) on an island on the Great Bahama Bank where they occur together. He reports that they occupy different microhabitats. Similar differences in microhabitats probably serve to reduce competition between sympatric anoles on Puerto Rico (Rand, 1964) and Jamaica (Rand, 1967a). In both Puerto Rico and Jamaica, differences in microhabitat between some species are reinforced by interspecific territorial defense (Rand, 1964, 1967b). Where one of these species is abundant and another rare, all of the available territories in the preferred microhabitat of the abundant species may be occupied by large adults, so that young individuals are forced to establish their territories in the microhabitat characteristic of the second species. These observations suggest that interspecific competition can occur even between species with different microhabitat preferences, particularly whenever one of the species is very abundant. We do know that on small islands the species present may be there in large numbers. One species of *Anolis* that occurs without congeners, *lineatus* on Curaçao, occupies a more varied microhabitat than do many populations of Greater Antillean species which occur sympatrically (Rand and Rand, 1967).

It is possible that successful colonizations of already inhabited islands were successful because the colonist landed at a time and in a place where the population density of established species was temporarily low. The larger and older the island and the more frequent the colonization attempts, the more likely it is that a colonist will land at a favorable time and place. This may explain the minor age, area, and position effects seen.

The difficulty of colonizing an inhabited island accounts for the very small number of species occurring on many of the small West Indian islands. This phenomenon of competitive exclusion may also help to account for the relatively small amount of anole interchange among the Greater Antilles themselves and to explain why their anole radiations have been largely independent of one another.

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(Received 7 November 1968.)

TABLE 1

Numbers of Species of Anolis on Various Islands in the West Indies

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
Islands fringing the Greater Antilles; 44 islands on 4 banks.		
Cuba	23	43,036.0
Isla de Piños	8	1,159.0
Hispaniola	21	28,242.0
Gonave	5	254.0
Ile Tortue	3	70.0
Ile Vache	3	20.0
Grand Cayemite	3	17.0
Beata	2	16.0
Saona	3	4.0
Pte. Cayemite	1	0.5
Jamaica	7	4,450.0
Bogue	1	0.25
Pigeon	1	0.125
Salt	1	0.125

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
Booby	1	0.062
Cabaritta	2	0.062
Emerald	1	0.062
Lime	1	0.062
Puerto Rico	10	3,421.0
Vieques	3	51.0
St. Thomas	3	32.0
Tortola	3	24.0
St. John	3	19.0
Anegada	2	15.0
Culebra	4	11.0
Virgin Gorda	3	10.0
Jost Van Dyke	2	5.0
Peter	3	3.0
Beef	2	2.0
Guana	3	2.0
Caja de Muertos	2	1.5
Water	3	1.0
Cooper	1	1.0
Savana	2	0.75
Salt	1	0.75
Hassel	1	0.5
Culebrita	1	0.5
Lovango	2	0.5
Little St. James	2	0.5
Fallen Jerusalem	2	0.5
Little Saba	2	0.25
Congo	2	0.25
Cockroach	1	0.25
Dutchman's Cap	1	0.25
Dead Man's Chest	1	0.25
Salt Key	1	0.25
Cayo Santiago	3	0.125
Dog	1	0.125
Lesser Antilles: 33 islands on 16 banks.		
Anguilla	2	35.0
St. Martin	2	35.0
St. Barthelmey	1	9.5
Antigua	2	108.0
Barbuda	2	62.0
Saba	1	5.0
St. Eustatius	2	7.7
St. Kitts	2	68.0
Nevis	2	50.0
Redonda	1	0.5
Montserrat	1	38.0

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
Désirade	1	10.5
Guadeloupe	1	687.0
Les Saintes, Terre de Bas	1	3.0
Terre de Haut	1	2.5
Marie-Galante	1	58.0
Dominica	1	305.0
Martinique	1	427.0
St. Lucia	1 (2 introduced)	233.0
Barbados	1	166.0
St. Vincent	2	133.0
Grenada	2	120.0
Quatres	1	0.5
Carriacou	2	8.0
Mustique	1	2.5
Petit Mustique	1	0.125
Petit Nevis	1	0.125
Baliceaux	1	0.75
Petit Martinique	1	1.0
Frigate	1	0.25
Ronde	1	1.0
Caille	1	0.25
Diamond	1	0.125
Isolated islands; 11 islands on 9 banks.		
St. Croix	1	82.0
Buck	1	0.75
Grand Cayman	1	71.0
Mona	1	21.0
Cayman Brac	1	13.0
Little Cayman	2	9.0
Navassa	1	1.5
Swan (Larger)	1	1.0
Swan (Smaller)	1	0.5
Desecheo	1	0.75
Alta Vela	1	0.5
Bahamas; 53 islands on 15 banks.		
Great Bahama Bank (15 islands)		
Andros	4	500.0
Eleuthera	4	164.0
Cat Island	4	160.0
Long Id	4	130.0
Great Exuma	4	108.0
Mangrove Cay	3	85.0
New Providence	4	58.0
Little San Salvador	1	4.25
Stocking Id	1	4.0

Island (those indented under another lie on the same bank)	Number of *Anolis* species	Island area in sq. mi.
South Bimini	4	3.0
North Cat Cay	2	0.75
Margaret Island, Ragged Island Group	1	0.75
Flamingo Cay	1	0.5
Knife Cay	1	0.062
Goat Cay	1	0.062
Acklins	1	185.0
Crooked Id	2	76.0
Long Cay	1	7.0
Castle Island	1	1.5
Cotton Cay	1	0.5
Atwood Cay	1	10.0
Grand Caicos	1	40.0
North Caicos	1	40.0
Providenciales	1	30.0
East Caicos	1	30.0
South Caicos	1	8.0
West Caicos	1	7.0
Pine Cay	1	1.0
Cotton Cay	2	2.0
Elbow Cay	1	1.0
Conception	1	4.0
East Plana Cay	1	3.0
Great Inagua	1	560.0
Sheep Cay	1	0.25
Little Bahama Bank		
Gr. Abaco Id	1	776.0
Grand Bahama	1	430.0
Little Abaco	1	27.0
Elbow Cay	1	2.0
Pensacola Cay	1	1.0
Water Cay, Grand Bahama	1	1.0
Strangers Cay	1	0.75
Moraine Cay	1	0.062
Little Inagua	1	45.0
Mayaguana Id	1	96.0
Booby Cay	1	0.25
Rum Cay	2	29.0
Grand Turk	1	8.0
Salt Cay	1	2.5
Cotton Cay	1	0.5
Long Cay	1	0.25
Great Sand Cay	1	0.25
Watlings Id	2	60.0
West Plana Cay	1	3.5